Quantifying the effects of commercial clam aquaculture on C and N cycling: An integrated ecosystem approach

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ABSTRACT

Increased interest in using bivalve cultivation to mitigate eutrophication requires a comprehensive understanding of the net carbon (C) and nitrogen (N) budgets associated with cultivation on an ecosystem scale. This study quantified C and N processes related to clam (*Mercenaria mercenaria*) aquaculture in a shallow coastal environment (Cherrystone Inlet, VA) where the industry has rapidly increased. Clam physiological rates were compared with basin-wide ecosystem fluxes including primary production, benthic nutrient regeneration, and respiration. Although clam beds occupy only 3% of the ecosystem's surface area, clams filtered 7-44% of the system's volume daily, consumed an annual average of 103% of the phytoplankton production, creating a large flux of particulate C and N to the sediments. Annually, N regenerated and C respired by clam and microbial metabolism in clam beds were ~3-fold and ~1.5-fold higher, respectively, than N and C removed through harvest. Due to the short water residence time, the low watershed load, and the close vicinity of clam beds to the mouth of Cherrystone Inlet, cultivated clams are likely subsidized by phytoplankton from the Chesapeake Bay. Consequently, much of the N released by mineralization associated with clam cultivation is 'new' N as it would not be present in the system without bivalve facilitation. Macroalgae that are fueled by the enhanced N regeneration from clams represents a eutrophying process resulting from aquaculture. This synthesis demonstrates the importance of considering impacts of bivalve aquaculture in an ecosystem context especially relative to the potential of bivalves to remove nutrients and enhance C sinks.

INTRODUCTION

Suspension feeding bivalves can significantly shift energy flow through an ecosystem, particularly in a high-density aquaculture setting (Dame 2011). As shellfish mariculture expands globally (FAO 2014), an understanding of the magnitude by which these operations alter fluxes of carbon (C) and nitrogen (N) in nearshore marine ecosystems is needed to ensure ecological as well as economic sustainability. Further, there has been growing interest in using the bioextraction associated with bivalve cultivation for nutrient trading (Stadmark and Conley 2011; Bricker et al. 2014; Petersen et al. 2014; Rose et al. 2014) and carbon sequestration programs (Filgueira et al. 2015). However, few studies have investigated the net influence of bivalve cultivation on an ecosystem scale, integrating the direct and indirect ecological feedbacks.

As suspension feeders, bivalves directly affect phytoplankton, ecosystem respiration, and nutrient availability. By consuming phytoplankton and detrital material from the water column, bivalves may exert 'top-down' control on phytoplankton primary production (Cloern 1982; Officer et al. 1982; Cohen et al. 1984; Strayer et al. 1999). The bivalves assimilate a fraction of this organic material, while another portion is respired; the rest is released as biodeposits to the sediments. As heterotrophic organisms, bivalves release dissolved inorganic carbon (DIC) (Chauvaud et al. 2003; Mistri and Munari 2012), and dissolved inorganic nitrogen (DIN) through respiration and excretion, respectively. However, actively growing bivalves also sequester C and N in their tissue and shell (Newell 2004; Tang et al. 2011; Beseres Pollack et al. 2013).

Bivalves also facilitate indirect ecological feedbacks in an ecosystem (as reviewed in Newell 2004). By delivering labile organic matter in the form of biodeposits to sediments,

bivalves fuel microbial processes (Mirto et al. 2000; Giles and Pilditch 2006). Microbial mineralization of biodeposits transforms particulate organic matter (POM) into dissolved organic and inorganic nutrients and carbon. Sediments associated with bivalve aquaculture are often enriched in organic content and have elevated porewater nutrient concentrations (Mesnage et al. 2007; Metzger et al. 2007). The dissolved nutrients regenerated from biodeposits may be released to the water column, where in addition to the nutrients from bivalve excretion, they can serve as an important source for primary producers (e.g. (Doering et al. 1987; Souchu et al. 2001; Murphy et al. 2015). Thus bivalves may indirectly facilitate 'bottom up' control on primary production.

Local physical characteristics such as water residence time, depth, and nutrient loading determine, to a large extent, the community composition of primary producers (Valiela et al. 1997a). They are also important factors that regulate the degree to which bivalves directly and indirectly alter C and N cycling. For example, if an aquaculture operation is located in a shallow photic system, the dominant primary producer fueled by the bivalve operation may be benthic microalgae, submerged aquatic vegetation, and/or macroalgae, as opposed to pelagic phytoplankton. This has direct consequences on bivalve growth, as these producers are typically not considered available for bivalve consumption (although, see Hondula and Pace 2014; Emery et al. 2015). Additionally, bivalve aquaculture located in a highly flushed system with a short residence time is likely subsidized by phytoplankton produced outside of the immediate ecosystem, modifying the energy budget within the system (Guyondet et al. 2013; Filgueira et al. 2014).

The majority of studies that have examined energy and nutrient flow associated with bivalve aquaculture have focused on organismal scale impacts neglecting the consideration of

84 context-dependent ecological feedbacks (e.g. support of additional production through nutrient
85 regeneration). These complex trophic interactions and indirect effects driven by bivalve
86 aquaculture are important components in assessing the net ecosystem effects of mariculture on C
87 and N cycling. Additionally, these interactions must be explored within the context of local site-
88 specific characteristics such as residence time and primary production as these affect how
89 bivalves alter energy flow in an ecosystem.
90 The objective of this study was to quantify hard clam (*Mercenaria mercenaria*)
91 aquaculture C and N processes relative to other basin-wide fluxes for a shallow coastal
92 ecosystem, Cherrystone Inlet, VA. We compare clam feeding, respiration, excretion, egestion,
93 and shell production to ecosystem processes such as benthic and pelagic primary production and
94 benthic microbial metabolism, including denitrification rates. We incorporate an ecosystem
95 framework accounting for the trophic interactions between the clams, phytoplankton,
96 macroalgae, and microbial community, while including clam harvest as a C and N loss from the
97 aquatic system. We hypothesize that the high densities of clams in Cherrystone Inlet significantly
98 alter the magnitude of C and N fluxes within the system given their capacity to filter a large
99 volume of the system.
100
101 **METHODS**
102 *Site Description and Clam Cultivation Practices*
103 Cherrystone Inlet is a small tidal embayment (5.6 km^2) on the western shore of the
104 Delmarva (Delaware-Maryland-Virginia) Peninsula in Virginia (Figure 1). The Inlet averages
105 1.1 m in depth (mean sea level; MSL) and is characterized by shallow flanking shoals with a
106 narrow channel that leads to the Chesapeake Bay (Reay et al. 1995). Although the entire

107 embayment is leased for shellfish production (Virginia Marine Resources Commission), active
108 leases only exist in the shallow subtidal portions of the bay (Emery 2015), with the majority of
109 this space occupied by hard clam (*Mercenaria mercenaria*) mariculture (Figure 1). The volume
110 of the embayment is $6.2x10^6$ m^3 (MSL) with a tidal prism of $4.5x10^6$ m^3 (Kuschner 2015). The
111 Inlet has an average hydrologic residence time of 2-3 days (Herman et al. 2007).
112 Typical clam cultivation practices in the US involve planting hatchery-reared juveniles in
113 subtidal sediments. Since all clams within a bed are planted concurrently, each clam bed
114 (typically in VA ~4m x18m) consists of a homogenous size-class. Growers place a plastic mesh
115 net flush to the sediment surface over each clam bed to protect the clams from natural predators
116 (e.g. blue crabs, cow-nose rays). Use of a predator-exclusion net is a common clam cultivation
117 practice throughout the US (Castagna 2001). In the warmer months, macroalgae typically recruit
118 onto the nets and proliferate, fueled by nutrient regeneration associated with the clams and
119 microbial processes in the sediments (Bendell 2015; Murphy et al. 2015). The macroalgae
120 significantly reduce flow across the sediment water interface (Adams et al. 2011) and are swept
121 off the nets by the aquaculturists approximately monthly to prevent detrimental effects to the
122 clams (T. Rapine, Cherrystone Aquafarms, pers. comm.).
123
124 *Water Quality*
125 Dataflow surface water quality mapping surveys, which were conducted throughout the
126 Inlet in March 2011, and May, July, and October 2012, measured surface water temperature, pH,
127 chlorophyll (chl), turbidity, and dissolved oxygen (DO). The dataflow system is equipped with a
128 YSI 6600 datasonde, which is calibrated prior to and after each survey, a Garmin global
129 positioning system, and data acquisition system (Madden and Day 1992). During each survey,

discrete surface water samples were collected for extractable chl analysis (Shoaf and Lium 1976) at six randomly selected stations across the embayment. The dataflow chl data were calibrated to these samples using linear regressions of *in situ* YSI chl measurements versus extractable chl. Chl data were visualized using ArcGIS 10.2 and the inverse distance-weighting tool (IDW) was used to create a spatially interpolated map of chl over the entire Inlet, for each of the four seasonal samples. The zonal statistics tool was used to compare chl in water directly over the clam beds with the rest of the Inlet to determine the effect of clams on proximal chl concentrations.

Clam Aquaculture Spatial Coverage

The standing stock of clams in Cherrystone Inlet was estimated using aerial image analysis. Clam beds are readily visible in photographs taken at low tide for the annual Submerged Aquatic Vegetation Survey conducted by the Virginia Institute of Marine Science (VIMS) (Orth et al. 2010). The clam beds (each 72 m^2), covered with anti-predator netting, appear as black rectangles in the images. Active clam leases were delineated in ArcGIS (ESRI) using photographs from 2001 and 2003 – 2012 and combined with prior estimates of clam aquaculture coverage for 1990-1997 (Woods 2001). A linear regression of the number of active clam beds and time was used to analyze industry trends from 1990-2012 and estimate the rate of expansion over time in Cherrystone Inlet.

The standing stock of clams in the system in 2012 was estimated by multiplying the surface area of clam beds, obtained from aerial photographs in 2012, by the clam density data collected in the field (see below). The surface area estimate included only the active clam beds in

152 the photographs and represents a conservative estimate of clam coverage that excludes the space
153 between clam beds and inactive beds.
154
155 *Clam Population Size Class Distribution*
156 Clam population and size distribution data, including density, mean shell lengths and
157 biomass, were obtained from sediment cores collected seasonally in 2013 across the largest lease
158 in Cherrystone Inlet. Triplicate sediment cores (9.5 cm inside diameter) were collected from
159 randomly selected clam beds in May (n=16), July (n=16), and November (n=7). In each core,
160 clams were counted, measured, and dry weights and ash-free dry weights were obtained.
161 An estimate of the total number of clams in the Inlet was obtained by multiplying the
162 average clam density (individuals m^{-2}) by the total areal extent of the clam beds in the Inlet (see
163 "Clam Aquaculture Spatial Coverage"). Clams were binned according to industry-designated
164 size categories as seed, button, littleneck, and middleneck. The mean shell length for each
165 category was determined by measuring the shell lengths of clams harvested and sold in these size
166 categories. The mid-point between the means of each size class served as the breakpoint from
167 one size class to the next in order to obtain a range for each size class. Button clams were
168 designated as 25.3 to 42.1 mm, littlenecks were 42.2 to 50.9 mm, and middlenecks were 60.0
169 mm and greater. Seed clams were designated as averaging 12 mm (T. Rapine, Cherrystone
170 Aquafarms, pers. comm.) and ranged from 0 to 25.3 mm. The total number of clams within each
171 size class was estimated using the size frequency distribution of the field survey data. For
172 example, the total number of littleneck clams within the Inlet was calculated as the percentage of
173 clams that were between 42.2 to 50.9 mm from the field data multiplied by the total number of
174 clams in the Inlet.

175

176 *Total C and N in Clam Standing Stock Population and Annual Harvest*

177 The relationship between shell length and soft tissue dry weight of a subset of clams
178 collected in the field (n = 159) was used to estimate the biomass (DW_{Tissue}; g DW individual^{-1})
179 for each size class (Supplementary Figure S1) as

180

181 $$DW_{Tissue} = 0.0009L^2 - 0.028L + 0.266 \quad (1)$$

182

183 where L is equal to shell length (mm). Biomass was scaled to the total population of each size
184 class and summed to obtain the total biomass of clams within the Inlet. Clam tissue samples were
185 collected seasonally in 2011-2012 from Cherrystone Inlet (N=90), dried and analyzed
186 individually for total N and organic C content on a Carlo-Erba elemental analyzer (Thermo
187 Electron Corp. Flash EA 1112 Series). Seasonal data were averaged to obtain an annual average
188 percent total N (9.05% +/- 0.13 standard error (SE)) and organic carbon (40.04% +/-0.38 SE).
189 The total C and N in the soft tissue of the clam standing stock was obtained by multiplying total
190 tissue dry weight by the average percent organic C and total N. A similar estimation was used to
191 determine the C and N removed annually through harvest (see below).

192 Shell dry weights (DW_{Shell}; g DW individual^{-1}) for each size class were estimated using
193 an equation derived from Wiseman (2010) as

194

195 $$DW_{Shell} = 0.0002L^{2.93} \quad (2)$$

196

where L is shell length (mm). DW_{Shell} were converted to inorganic and organic carbon assuming approximately 95% of the shell weight is calcium carbonate (Vinogradov 1953, Bouillon et al. 2011) of which 12% is inorganic carbon by mass. Approximately 1.9% of the shell weight is organic carbon (Price et al. 1976; Doering et al. 1987; Bouillon et al. 2011) and 0.2% is N (Carmichael 2004). Inorganic and organic C in the tissue and shell were summed to estimate the total C stored in the Inlet's living clam population.

The total number of individuals within each size class harvested from Cherrystone Inlet in 2012 was obtained from local growers and used to calculate the amount of C and N removed annually in clam tissue and shell material using the relationships described above.

Clam Physiological Rates

Clam physiological rates were calculated using equations from the literature and scaled to the seasonal standing stock clam population in Cherrystone Inlet in 2012. Specific equations are summarized in Supplementary Table S1 and briefly described below. Physiological rates were calculated for each of the four size classes (i.e. seed, button, littleneck, and middleneck) using measured environmental data from each season (winter, spring, summer, and fall) and scaled to seasonal and annual rates.

Filtration rates (FR, ml ind^{-1} d^{-1}) were estimated using equations from Hofmann et al. 2006 and modified by Wiseman 2010 in which the maximum filtration rate (FR_{max}, ml ind^{-1} d^{-1}), originally derived from an equation by Doering and Oviatt (1986), was adjusted by dimensionless functions to account for the effects of temperature and salinity. Additionally, the predator exclusion nets in Cherrystone Inlet were found to reduce filtration rates by 35% (Condon 2005); therefore, our rates were reduced to account for this local cultivation effect.

Filtration rates were converted to total ingestion rates of particulate N and particulate C of the clam standing stock (g PN and g PC day^{-1}) using the mean seasonal chl concentrations across the Inlet measured during the dataflow surveys, the ratios of PN and PC to chl (7.03 g N g chl^{-1} and 57.21 g C g chl^{-1}, respectively) obtained using water column data collected by the VA Department of Environmental Quality directly outside of Cherrystone Inlet (monitoring station CB 7.3), and the total number of clams within each size class in the system.

Clam respiration rates were estimated using an equation from Hofmann et al. (2006) adjusted by Wiseman 2010 using data collected in Cherrystone (Condon 2005). Rates of clam excretion, primarily composed of NH_4^+ (Hammen 1980), were calculated based on stoichiometry (Mayzaud and Conover 1988), using a ratio of respiration to excretion for *M. mercenaria* of 7.83. This ratio was obtained in an experiment conducted in July 2013, in which Cherrystone clams of varying sizes were incubated in closed chambers without sediments and fluxes of oxygen and NH_4^+ were measured (Supplementary Data, Figure S2).

Egestion rates were estimated using an assimilation efficiency fixed at 75%. Although assimilation efficiency is dependent on seston quality and quantity (Bass et. al 1990, Secrist 2013), this estimate is reasonable for Cherrystone Inlet based on findings from a clam growth model specific to Cherrystone Inlet where this assimilation rate produced realistic weights and growth rates (Kuschner 2015) and is supported by literature findings for *M. mercenaria* (Tenore et al. 1973).

Primary Production

241 Seasonal macroalgal, benthic microalgal, and phytoplankton net production rates and N
242 demands were estimated using data collected in Cherrystone and reported in previous studies
243 (Reay et al. 1995; Murphy et al. 2015; Kuschner 2015).
244 The macroalgal community on the predator exclusion nets is typically dominated by
245 *Gracilaria* spp., intermixed with *Ulva lactuca* and *Agardhiella* spp. (Murphy et al. 2015).
246 Murphy et al. (2015) provide seasonal benthic *in situ* flux data from 2012 at clam beds in
247 Cherrystone Inlet with and without the addition of macroalgae. These data were used to
248 calculate macroalgal production and N uptake rates; details on the approach are provided in
249 Murphy et al. (2015). Macroalgal production and N demand rates were scaled to the estuary by
250 multiplying by the total areal coverage of clam nets. Self-shading effects on macroalgal
251 production and N demand were not considered important as aquaculturists sweep the nets
252 frequently, maintaining a biomass (24-124 g DW m^{-2}; Murphy et al. 2015) generally lower than
253 when self-shading becomes significant (>100 g DW m^{-2}; McGlathery et al. 2001).
254 Benthic metabolic rates in sediments outside of the cultivation areas were used to
255 estimate benthic microalgal production and N demands (Reay et al. 1995; Murphy et al. 2015).
256 Reay et al. (1995) report seasonal *in situ* flux measurements in 1990-1991, prior to the expansion
257 of clam beds in the system. Therefore, these measurements may be considered an estimate of
258 baseline benthic metabolism and nutrient fluxes that have not yet been altered by clam
259 aquaculture. Conversely, the sediment fluxes reported by Murphy et al. (2015) in control areas
260 outside of the clam beds have presumably been affected by at least two decades of clam
261 aquaculture in the system. These two studies, which were conducted using similar methods,
262 provide an opportunity to compare benthic processes before and after clam cultivation was
263 established. Benthic microalgal production rates were estimated using the benthic gross primary

production rates reported in Reay et al. (1995) and Murphy et al. (2015) and adjusting for autotrophic respiration, assumed to be 10% of production (Cloern 1987). As rates were measured during peak irradiance hours during the day, values were adjusted using a P-I curve model described by (Pinckney and Zingmark 1993), which accounts for diel light variation (measured in the field) on benthic microalgal production. Production rates were converted to N demand using a molar C/N ratio of benthic microalgae of 9.0 (Sundbäck et al. 2000). These rates were scaled to the estuary by multiplying by the total surface area of the Inlet, assuming the majority of the sediments are photic. This assumption is reasonable as the average depth of the system is 1.1 m, and Reay et al. (1995) report the photic zone, in which >1% of the surface irradiance reaches the sediment surface, to be from 0.7m in the summer to 6.1m in the winter.

Phytoplankton production rates were obtained from an ecosystem model described by Kuschner (2015). Briefly, an ecosystem box model applicable to shallow coastal systems (Brush 2002, Lake and Brush 2015) was adapted to Cherrystone Inlet using forcing data specific to the system (e.g. temperature, salinity, TSS, photosynthetically active radiation (PAR)). Phytoplankton primary production was modeled as a function of chlorophyll-a biomass (B), photic depth (Z_p), and PAR (I_0) using the empirical "BZ_pI_0" relationship that applies well to temperate estuaries (Brush et al. 2002; Brush and Brawley 2009). Production computed using the BZ_pI_0 approach is generally interpreted as representing net daytime production (Brush et al. 2002); rates were converted to GPP assuming dark respiration consumes 10% of GPP (Laws and Bannister 1980; Foreman 1985; Valiela 1995). Model calibration was conducted by Kuschner (2015) using water quality data collected by the Chesapeake Bay Program (VA Department of Environmental Quality) at the three monitoring stations within Cherrystone Inlet during 2001-2002.

287

288 *Benthic Microbial Respiration and N Mineralization*

289 Microbial respiration and net N mineralization rates were estimated in the clam
290 cultivation sediments and control sediments (i.e. outside the cultivation areas) using seasonal *in*
291 *situ* benthic flux data from 2012 (Murphy et al. 2015). The microbial contribution to N
292 remineralization and respiration at the clam beds was estimated by subtracting the calculated
293 clam excretion and respiration rates from the dissolved N fluxes and benthic respiration at the
294 clam beds (Murphy et al. 2015); these values were scaled to the surface area of the clam beds in
295 Cherrystone in 2012. Respiration and dissolved N flux rates at the uncultivated sediments,
296 reported by Murphy et al. (2015), were scaled to the surface area of the embayment minus the
297 clam bed area.

298

299 *Watershed Loading and Net Exchange with Chesapeake Bay*

300 Watershed loading of total nitrogen (TN) was computed by Kuschner (2015) using the
301 Nitrogen Loading Model (NLM) of Giordano et al. (2011), based on the original NLM
302 developed by Valiela et al. (1997b). Briefly, the model computes mean annual TN loading from
303 atmospheric deposition onto various land uses, fertilizer application, agricultural activities (crops
304 and poultry), and leaching from septic tanks, with bulk coefficients for attenuation through
305 vegetation, ponds, the vadose zone, and the aquifer. The model was adapted to the Virginia
306 Eastern Shore by Giordano et al. (2011), and to the watershed of Cherrystone Inlet by Kuschner
307 (2015).

308 Exchanges with Chesapeake Bay were obtained from the ecosystem model of Kuschner
309 (2015). The model computes daily volumetric exchanges based on the surface area of

310 Cherrystone Inlet and the mean tidal range at Kiptopeke, VA (tidesandcurrents.noaa.gov),
311 assuming two flooding and two ebbing tides per day. These exchanges were multiplied by
312 modeled DIN concentrations and phytoplankton biomass within Cherrystone to compute export
313 to the Chesapeake Bay, and by forced boundary conditions outside the system from Chesapeake
314 Bay Program monitoring station CB7.3E to compute import from the Chesapeake. Net exchange
315 of phytoplankton biomass was converted to particulate N using a Redfield C:N ratio of 6.625.
316
317 RESULTS
318 *Environmental Characteristics - 2012*
319 In 2012, water temperature ranged from an average of 7.1°C in the winter (Dec-Feb) to
320 27.5°C in the summer (Jun-Aug). Salinity varied little across the year, with slightly lower
321 salinity in the spring and summer than the fall and winter months (Table 1). Chl concentrations
322 were highest in the spring at 15.2 $\mu g\ l^{-1}$ and lowest in the winter at 1.8 $\mu g\ l^{-1}$. POC and PN
323 varied similarly throughout the year with lowest values in the winter and highest values in the
324 spring and summer (Table 1).
325 The dataflow surveys provide a seasonal spatial snapshot of water quality parameters
326 across the Inlet in 2012. As shown in Supplementary Table 2, mean chl, pH, DO, and turbidity
327 were generally lower in the regions with clam beds than the uncultivated regions of the estuary,
328 but these trends were statistically significant only for turbidity. Additionally, the spatial
329 distribution of chl does not show a clear draw down over the clam beds (Figure 2). This is likely
330 due to sampling logistics; the boat running the dataflow system could not drive over the clam
331 beds, as the areas were too shallow to navigate (note the shiptracks in Figure 2). As such, the
332 spatial resolution of the dataflow surveys is limited and likely does not fully capture the effect of

clam filtration on water quality. Notably, as illustrated in Figure 2 chl was typically highest in the upper regions of the estuary, particularly in the summer.

Clam standing stock population and harvest

There were 2,514 clam beds in Cherrystone Inlet in 2012. Overall clam aquaculture coverage in Cherrystone Inlet has significantly increased since 1989 (Figure 3, $R^2 = 0.77$, $p < 0.001$) with an annual clam bed growth rate of about 104 beds per year. Clam standing stock, total biomass, and harvest information from 2012 are provided in Table 2. In 2012, the clam biomass to water volume ratio in Cherrystone was 12.5 g DW m^{-3}. The total C and N contained within the clam standing stock was 210 megagrams (Mg) C and 10 Mg N. About 21% of the clam population is harvested annually, equating to about 45% of the total C and N contained in clam standing stock biomass, since the larger clams are harvested (Table 2). Approximately 96.6 Mg C and 4.5 Mg N is removed from the aquatic system annually through clam harvest.

Clam Physiological Rates-2012

Total filtration rates of the clam population in Cherrystone ranged from 0.4×10^6 m^3 day^{-1} in the winter to 2.8×10^6 m^3 day^{-1} in the fall with intermediate rates in the spring and summer (Table 3). With this filtration capacity, the number of days it took the cultivated clam population to filter a volume of water equal to that of the whole system ranged from 2.3 to 14.5 days (Table 3); between 20 and 124% of the tidal exchange was filtered each day (2 tides per 24 hr).

Table 4 summarizes the seasonal clam physiological rates (ingestion, respiration, excretion, egestion, and assimilation). Similar to filtration rates, clam ingestion rates also varied seasonally; however, despite highest filtration rates in the fall, highest ingestion rates occurred in

356 the summer months when water column PC and PN concentrations were elevated (Table 1).
357 Highest ingestion rates were 1905.5 kg C day^{-1} and 287.6 kg N day^{-1}, while lowest rates,
358 measured in the winter, were 43.9 kg C day^{-1} and 6.6 kg N day^{-1} (Table 4).
359 Clam respiration rates ranged from 59.2 kg C day^{-1} in the winter to 462.6 kg C day^{-1} in the
360 summer. Similarly excretion rates were highest in the summer at 59.1 kg N day^{-1} and lowest in
361 the winter at 7.6 kg N day^{-1} (Table 4). On an annual basis approximately 28% of the assimilated
362 C was respired by the clams and released as DIC while approximately 21% of the assimilated N
363 was excreted as NH_4^+. Our clam energetics model set biodeposition rates at a constant of 25% of
364 ingested C and N as assimilation was assumed to be 75%. Therefore egestion followed similar
365 seasonal trends as ingestion, with rates ranging from 11.0 kg C day^{-1} in the winter to 476.4 kg C
366 day^{-1} in the summer.
367
368 *Primary Production*
369 Phytoplankton net production ranged from 0.08 to 0.36 g C m^{-2} d^{-1} throughout the Inlet,
370 with an annual rate of 69.1 g C m^{-2} yr^{-1}. Phytoplankton turnover time (i.e. biomass:production)
371 computed using simulated biomass from Kuschner (2015) ranged from 1.3 to 3.6 days, with an
372 annual average of 2.4 days (Table 5). Scaled to the entire system, phytoplankton production
373 rates ranged from 0.42 Mg C d^{-1} in the winter to 2.0 Mg C d^{-1} in the summer with an overall
374 annual production of 389.0 Mg C yr^{-1} (Table 6). Clams were estimated to ingest 10%, 124%,
375 96%, and 147% of the net phytoplankton production in winter, spring, summer, and fall,
376 respectively. Annually, clams consumed an average of 103% of the net phytoplankton
377 production (Table 6).

Macroalgal net production rates on the clam cultivation nets ranged seasonally from 1.5 to 4.3 g C m^{-2} d^{-1}, with an annual production rate of 825.3 g C m^{-2} yr^{-1}, assuming zero macroalgal production in the winter (no winter data available). Scaled to the total surface area of the clam nets in the Inlet, macroalgal net production rates ranged from 0.28 Mg C d^{-1} in the fall to 0.77 Mg C d^{-1} in the summer, with an overall annual production of 149.4 Mg C yr^{-1} (Table 6).

Historical BMA net production rates, estimated using Reay et al. (1995) data collected in 1990-1991, ranged from 0.06 to 0.20 g C m^{-2} d^{-1}, with an annual production of 53.0 g C m^{-2} yr^{-1}. These rates were lower than BMA net production rates obtained in 2012 (Murphy et al. 2015), which ranged between 0.81 and 1.04 g C m^{-2} d^{-1} with an annual production of 230.2 g C m^{-2} yr^{-1}, although winter data were not available for this dataset. Scaled to the entire ecosystem, assuming the sediments are photic throughout the year (Reay et al. 1995), total BMA production rates were 298.2 Mg C yr^{-1} in 1990-1991 and 1295.6 Mg C yr^{-1} in 2012 (Table 6).

Benthic Respiration and N Remineralization Rates

For the uncultivated sediments (area outside of the clam beds), respiration, scaled to the surface area of the Inlet, ranged from 1.3 Mg C d^{-1} in spring to 3.1 Mg C d^{-1} in fall, with summer rate of 1.4 Mg C d^{-1} (Figure 4A). Total clam bed respiration rates, including both clam and microbial respiration, scaled to the surface area of the clam beds, ranged from 0.37 Mg C d^{-1} in the fall to 0.65 Mg C d^{-1} in the spring and 0.43 Mg C d^{-1} in the summer (winter data not available). Total clam bed respiration rates averaged 31% of the uncultivated benthic respiration rates, despite clam bed surface area accounting for only 3% of the total system surface area.

Seasonal net NH_4^+ fluxes scaled to the surface areas of the uncultivated sediments and clam beds are provided in Figure 4B. Uncultivated sediments had a net NH_4^+ efflux in the spring

401 and fall and a net uptake in the summer. Again, despite occupying only 3% of the total system
402 surface area, the clam bed net NH_4^+ effluxes were much higher than at the uncultivated
403 sediments (Figure 4B). The NH_4^+ regenerated at the clam beds was 60%, 324%, 306%, and
404 233% that of total PN removed through harvest (i.e. 4.5 Mg N yr^{-1} or 0.012 Mg N d^{-1}) in the
405 winter, spring, summer, and fall, respectively.
406
407 *Exchange with the Chesapeake Bay*
408 The DIN and phytoplankton exchange between the Chesapeake Bay and Cherrystone
409 Inlet revealed large annual fluxes across the mouth. A net import of 3.0 Mg N-DIN was
410 observed with a gross import of 55.1 and export of 52.1 Mg N-DIN. There was a net export of
411 phytoplankton from Cherrystone Inlet to the Chesapeake Bay of 6.9 Mg PC and 1.0 Mg PN.
412 However, when the model was run without clams the net export was 46.5 Mg PC, demonstrating
413 the role clams play in retaining a large amount of PC that is advected into Cherrystone Inlet.
414
415 *Annual C and N Budget*
416 Annual fluxes of C and N associated with clam aquaculture as well as internal
417 phytoplankton production and exchange with the Chesapeake Bay are provided in Figure 5.
418 Clam ingestion rates of PC and PN are approximately 103% of the annual net phytoplankton
419 production. Of the PC and PN ingested by the clams, 25% is egested as biodeposits into the
420 sediments. About half the egested PC and PN is respired and remineralized by microbial
421 processes; the remainder is either buried or resuspended and transported away from the shallow
422 clam beds. Of the C and N that are assimilated by the clams, 15-30% is subsequently respired
423 and excreted by the clams. Annual harvest accounts for 24% and 7% of the PC and PN ingested

424 by the clams, respectively. Notably, as reported above only 20% of the clam population is
425 harvested each year, a reasonable estimate since it takes on average two years for clams to reach
426 market size, and the industry reports ~40% mortality (pers. comm. T. Rapine, Cherrystone
427 Aquafarms). The harvest numbers reported here only include the three major clam producers in
428 the system, several small scale operations were not accounted for in harvest totals.
429
430 DISCUSSION
431 This synthesis study demonstrates that high densities of clams considerably alter C and N
432 cycling in the Cherrystone Inlet ecosystem. Although the aerial footprint of clam cultivation
433 only occupies 3% of the total surface area of the embayment, the cultured clam population has
434 the capacity to filter a large portion of the water column daily (7-44%), resulting in a
435 considerable flux of PC and PN from the water column to the sediments. By shifting energy
436 from the water column to the benthos, clam cultivation alters fundamental ecosystem processes
437 such as primary production, respiration, and nutrient cycling (Peterson and Heck 1999, Grizzle et
438 al. 2001). A comparison between rate processes (i.e. respiration, net community production, and
439 NH_4^+ flux) at the clam bed and uncultivated sediments revealed that even after scaling to the
440 entire estuary, aquaculture strongly influenced benthic rates despite the relatively small surface
441 area the clam beds occupy (Figure 4).
442 Few studies have investigated the overall effect of bivalve cultivation on C and N budgets
443 on an ecosystem scale, with many focusing on the scale of the organism (e.g. Munari et al. 2013)
444 or farm (e.g. Ferreira et al. 2007). Additionally, the majority of previous research has focused on
445 the influence of epifaunal bivalves (i.e. mussels and oysters) on C and N dynamics (e.g.
446 Guyondet et al. 2013, Filgueira et al. 2014) with very few investigating infaunal clam cultivation

447 (although see Nizzoli et al. 2006, 2011, and Bartoli et al. 2001). As clam cultivation continues to
448 expand in Cherrystone Inlet, as well as worldwide, an understanding of its interactions with the
449 environment, specifically with respect to energy flow and N cycling, is necessary to avoid
450 negative ecological (e.g. local eutrophication) and economic (e.g. decreased production due to
451 carrying capacity issues) consequences.
452
453 *Budget Uncertainties*
454 A number of uncertainties are inherent in our estimates when scaled to the entire system,
455 particularly with respect to spatial and temporal environmental variability. However, the
456 objective of this study was not to estimate statistical uncertainty, but rather to compare the
457 relative magnitudes of ecosystem C and N cycling processes. While a more precise budget
458 would need to encompass uncertainty, our analysis indicates at a first order that key ecosystem
459 fluxes at an intensive clam cultivation site are large relative to background flux levels.
460 Despite uncertainties, our estimates are similar to those made by prior studies of
461 Cherrystone Inlet (Luckenbach and Wang 2004; Condon 2005). Luckenbach and Wang (2004)
462 reported that the clam standing stock in Cherrystone Inlet filtered approximately 28% of the tidal
463 exchange, requiring an average of 10 days to filter the system, while Condon (2005) estimated
464 that 10-82% of the total Inlet is filtered daily by the clam population. These rates are comparable
465 to our estimates that the clams filtered 10-62% of the tidal exchange and 7-44% of the total Inlet
466 volume daily, requiring 2.3-14.5 days to filter the entire system, depending on the season.
467 Modest differences between our findings and those reported by Luckenbach and Wang (2004)
468 and Condon (2005) likely stem from using different volume, surface area, and tidal prism data.
469 We used data from Kuschner (2015), whereas Luckenbach and Wang (2004) and Condon (2005)

utilized a larger spatial footprint for Cherrystone obtained from Kuo et al. (1998), which includes a broad area outside the mouth of the estuary where there is a sand spit that periodically encloses the outlet.

A more notable difference between our results and prior studies is that we estimate 4.5 Mg N yr^{-1} for harvested clam PN while Luckenbach and Wang (2004) derived a much larger estimate of 18 Mg N yr^{-1}. This discrepancy is mainly due to differences in assumed harvested clam sizes. The average harvested clam size used by Luckenbach and Wang (2004) was approximately 73 mm shell length, which is much larger than our harvested clam size, which ranged from 38.5 to 56.1 mm shell length (button to middleneck sizes). We obtained our values directly from the growers. Corroborating our estimated annual PN harvest (4.5 Mg N yr^{-1}) was a similar estimate by Condon (2005), which ranged from 2.4 to 5.5 Mg N yr^{-1}.

Clam Grazing, Internal Production, and External Inputs

In Cherrystone Inlet, the cultured clam population has a strong effect on phytoplankton biomass as the clams annually graze an average of 103% of the estimated phytoplankton production in the system. Theoretically, if the time it takes the bivalve community to filter the entire system (total clearance time) is approximately equal to the phytoplankton turnover time and shorter than the system residence time, the bivalve population will control phytoplankton biomass (Dame and Prins 1998), as occurs in northern San Francisco Bay (Cloern 1982). Numerous other studies have demonstrated cultivated bivalve populations exert top-down control on phytoplankton (e.g. Grant et al. 2008). For example, Souchu et al. (2001) found grazing by cultivated oysters in a poorly flushed lagoon in the Mediterranean controlled phytoplankton, except in the summer when nutrient regeneration supported additional phytoplankton production.

493 In Cherrystone, the clam clearance time (~2.3-14.5 days) is generally greater than the
494 phytoplankton turnover time (~1.3-3.6 days) and the system's residence time (~2-3 days),
495 implying that internal production may be sufficient to support current clam production.
496 However, the clam population was capable of grazing over 100% of internal phytoplankton
497 production, particularly in the spring (124%) and fall (147%). This assumes clams have
498 continuous access to the internally produced phytoplankton, which is not likely in Cherrystone
499 Inlet where the majority of clam beds are located close to the mouth of the Inlet (Figure 1),
500 whereas, chl concentrations are highest up-estuary (Figure 2). This spatial variation in chl may
501 be due to clam grazing, which depletes chl in adjacent waters; however, in a system like
502 Cherrystone Inlet, with a short residence time and high tidal forcing, advection is an important
503 process controlling chl distribution (as reviewed in Prins et al. 1998). Thus the clam population,
504 particularly in the outer portion of the Inlet, is likely fueled by phytoplankton delivered from the
505 Chesapeake Bay on incoming tides. Modeling, Kuschner (2015) supports this hypothesis,
506 demonstrating that if exchange with Chesapeake Bay were removed from their model, clam
507 growth would be reduced by approximately 40%, implying that the incoming tide provides an
508 important food subsidy for the cultured clams. Although the modeled PC and PN exchange with
509 the Chesapeake Bay revealed a small net export of phytoplankton from the system (Figure 5),
510 this is likely due to higher chl in Cherrystone Inlet than in the lower Chesapeake Bay due to
511 differences in depth and basin volume.
512 Although bivalves may be considered a natural control for eutrophication due to their
513 removal of phytoplankton (Officer et al. 1982), bivalves may also promote local eutrophication
514 (*sensu* Nixon 1995) indirectly by stimulating primary production by BMA, macroalgae, and/or
515 seagrass (as reviewed in Newell 2004; Dumbauld et al. 2009). In Cherrystone Inlet, clam

516 cultivation may promote BMA and macroalgal production by alleviating nutrient and/or light
517 limitation, thereby altering benthic fluxes. A comparison between benthic rate measurements
518 collected prior to the rapid expansion of clam cultivation in Cherrystone Inlet in 1990-1991
519 (Reay et al. 1995) with data collected in 2012 (Murphy et al. 2015) revealed BMA production in
520 sediments outside of the cultivation area has increased about 4-fold. This increase in benthic
521 primary production may be due to a general decrease in light attenuation in the system,
522 potentially a direct effect of clam filtration activity. Between 1990-91 and 2012 average
523 seasonal light attenuation decreased by an average of 46% (Supplemental Figure S3) (Reay et al.
524 1995; Murphy et al. 2015), which may be attributed to the increased clam cultivation in the
525 system (Peterson and Heck 2001, Newell et al. 2002, Newell and Koch 2004). Additionally,
526 over time the active drawdown of particulates to the sediments by clam feeding may enrich the
527 benthos with organic matter and nutrients, fueling BMA production (Newell et al. 2002).
528 Macroalgal production on the shallow predator exclusion nets associated with cultivation
529 operations is comparable to production of BMA and phytoplankton even when scaled to the
530 entire ecosystem. Clam cultivation provides both a hard substrate for macroalgal attachment as
531 well as a nutrient source for macroalgal growth (Powers et al. 2007; Murphy et al. 2015). As
532 highlighted in Figure 5, the clam beds are a large source of NH_4^+ to the water column due to both
533 clam excretion and microbial N mineralization. This increase in N regeneration was sufficient to
534 meet the entire N demand of the macroalgae proliferating on the nets (Murphy et al. 2015). In
535 turn, detrital macroalgal material is an important food source for cultivated clams (Secrist 2013;
536 Hondula and Pace 2014), which the current study did not consider.
537
538 *Implications of Nitrogen Cycling and Removal*

539 The concept that grazers may control eutrophication (i.e. the increased supply of organic
540 matter to a system, Nixon 1995) directly by exerting top-down control on phytoplankton is not
541 new (e.g. Cloern 1982; Officer et al. 1982; Dame and Prins 1998; Prins et al. 1998). However,
542 recently the debate has shifted to include the effects of bivalves on N removal and thus,
543 indirectly, eutrophication control (e.g. Stadmark and Conley 2011; Rose et al. 2011; Petersen et
544 al. 2011). Bivalve aquaculture has been suggested as an effective means to mitigate nutrient
545 pollution and reduce eutrophication risk (Lindahl et al. 2005; Bricker et al. 2014; Rose et al.
546 2014), since cultivation methods do not require feed input and upon harvest, N sequestered in the
547 bivalve tissue and shell is removed from the aquatic environment. However, this removal term
548 should be assessed relative to the enhanced nutrient regeneration associated with bivalve
549 cultivation to determine the overall effect of intensive bivalve culture on the ecosystem N budget
550 (Stadmark and Conley 2011 and 2012; Nizzoli et al. 2011).
551 In Cherrystone Inlet inorganic N regenerated in the clam sediments is ~3-fold higher than
552 the removal of N via harvest on an annual basis (approximately 14 vs. 4.5 Mg N yr^{-1}; Figure 5),
553 which tends to be lower than reported for other clam aquaculture systems, although very few
554 studies have made this comparison. In the Sacca di Goro, Italy, the sediment-water NH_4^+ fluxes
555 associated with clam aquaculture were more than 10-fold the amount of N removed through clam
556 harvest (Bartoli et al. 2001). Similarly, a study, which constructed an N budget for a system
557 dominated by mussel aquaculture, found cultivated mussels in Tracadie Bay, Canada directed 20
558 times more N to the water column and sediments through excretion and egestion, respectively,
559 than was harvested (Cranford et al. 2007). Stadmark and Conley (2011) argued that an
560 understanding of the changes in nutrient regeneration caused by bivalve aquaculture is critical to
561 determine the effectiveness of bivalves in nutrient removal. Alternatively, Rose et al. (2011)

562 noted that the nutrients recycled in sediments associated with bivalve cultivation (specifically,
563 mussels in the Baltic Sea) are ultimately sourced from primary production within the ecosystem.
564 However, this assumption cannot be applied to all bivalve cultivation operations, and in fact
565 considering the origin of the regenerated N is critical in determining the influence of the bivalves
566 on N removal.

567 In Cherrystone, the origin of the regenerated N, which fluxes from the clam sediments,
568 dictates the overall impact of clam cultivation on the ecosystem N budget. For example, if the
569 dominant food source for the clams is produced internally then N regeneration facilitated by the
570 clams, is a recycling of particulate N to dissolved N that was already in the system (i.e. no net
571 effect). However, if the PN filtered by the clams is drawn from outside the system, the
572 regenerated N facilitated by the clams is considered 'new' to the ecosystem, and would not be
573 delivered to the sediments in the absence of clam cultivation. As discussed above, the origin of
574 food (PN and PC) for the clams (i.e. internal vs. external) is dependent on the total clearance
575 time of the clam population relative to the hydrologic residence time and internal phytoplankton
576 production turnover time (Dame and Prins 1998). Due to the short residence time, the high clam
577 biomass to water volume ratio (12 kg m^{-3}), and the distribution of clam cultivation in outer
578 portions of the embayment, the system is likely functioning as a 'feedlot' as reviewed in Dame
579 (2011). Every incoming tide brings more Chesapeake Bay-sourced-phytoplankton to the clams,
580 which filter this material and facilitate its transformation to dissolved inorganic forms. In an
581 analysis of 11 coastal ecosystems dominated by bivalves, Dame and Prins (1998) reported
582 bivalve populations in three systems, Marennes-Oleron Bay, France (oysters and mussels), South
583 San Francisco Bay, US (invasive clams), and North Inlet, South Carolina, US (oysters), relied on

584 phytoplankton advected from outside the immediate system as the bivalve clearance time
585 exceeded water residence time or phytoplankton turnover time.
586 Another N removal process that is often associated with bivalve aquaculture is
587 denitrification, the microbial process that reduces NO_3^- to N_2. Although site-specific, numerous
588 studies have reported elevated denitrification rates in bivalve-dominated sediments, facilitated by
589 the increased organic matter deposition through bivalve egestion (Newell et al. 2002; Kellogg et
590 al. 2014; Nizzoli et al. 2006). For comparison to other fluxes, the seasonal denitrification rates at
591 clam beds in Cherrystone Inlet reported by Murphy et al. (in press) are included in our annual N
592 budget (Figure 5). Denitrification is small compared to N regeneration rates and N removal
593 through harvest, only accounting for 0.05% of the particulate N filtered by the clams and 0.2% of
594 the particulate N egested by the clams.
595
596 *Implications of Carbon Cycling and Removal*
597 Bivalve filter feeders can greatly alter the flow of carbon through a system, especially
598 when cultivated in large numbers (Dame and Prins 1998; Dumbauld et al. 2009; Tang et al.
599 2011; Filgueira et al. 2014; Filgueira et al. 2015). Our estimates of carbon fluxes in Cherrystone
600 Inlet associated with clam aquaculture highlight several of these pathways (Figure 5). A large
601 amount of carbon is removed from the water column through ingestion and is either assimilated
602 into the clam tissue, respired, or transferred to the benthos as feces and/or pseudofeces. As
603 described above, the transfer of particulate matter to the sediments can lead to improved water
604 clarity and stimulate benthic algal production. However, there are also ecological implications
605 related to the respired and assimilated carbon.

606 The respired carbon is released to the local environment as DIC. An additional source of
607 CO_2 from clams results from the calcification process where approximately one molecule of CO_2
608 is produced for each molecule of $CaCO_3$ produced (Frankignoulle and Canon 1994; Hily et al.
609 2013). Significant CO_2 production has been observed in large bivalve populations (Chauvaud et
610 al. 2003; Mistri and Munari 2012), yet there are possible abatement factors to this CO_2
611 production including stimulating the production of macroalgae (Murphy et al. 2015) and the use
612 of 5-37% of respired CO_2 as the inorganic carbon source in the shell building process (Gillikin et
613 al. 2007). Depending on system characteristics, a subsequent loss of CO_2 through gas transfer to
614 the atmosphere is possible and would represent a loss from the system. This may occur naturally
615 depending on the CO_2 saturation state of the system, but is potentially enhanced through shellfish
616 aquaculture (Chauvaud et al. 2003; Mistri and Munari 2012).
617 A second loss of carbon from the system occurs through harvest of the assimilated carbon
618 in shell and tissue material (Tang et al. 2011). While clam tissue is likely consumed and respired
619 on a short time scale, the fate of shell material is not as certain. In some cases shells are returned
620 to coastal systems for aquaculture or restoration purposes (Piazza et al. 2005). However, shells
621 are also largely disposed of on land, representing a potentially long-term carbon sink (NRC
622 2010). Also, consistent withdrawals of calcium carbonate through harvests can reduce alkalinity
623 thereby increasing the potential for acidification of the system (Waldbusser et al. 2013). Given
624 the impacts of aquaculture estimated in this study, developing improved carbon budgets for
625 systems with and without shellfish aquaculture is warranted to improve understanding of coastal
626 carbon cycling (Doney 2010; Cai 2011; Bauer et al. 2013; Laruelle et al. 2014; Filgueira et al.
627 2015; Gruber 2015).
628

Conclusions

Linking bivalve physiology, the physical environment, and ecosystem level processes to determine the overall effects of bivalves in a system is not a new concept; however, few recent studies that attempt to assess bivalves in terms of nutrient removal and carbon cycling fully consider the bivalves within the context of an ecosystem. This synthesis demonstrates the large influence clam cultivation has on C and N cycling, highlighting the importance of external food sources in supporting high biomass of clams in a system with a short water residence time. Although a net sink for PN and PC from the aquatic system upon harvest, bivalve aquaculture enhances benthic respiration and N mineralization on a local ecosystem scale. Depending on the physical characteristics of the ecosystem (e.g. residence time, depth, etc), food for clams may be derived from outside the immediate system (i.e. a subsidy). Thus the increased N mineralization associated with the bivalve cultivation is 'new' N as it would not be present in the system without the influence of the bivalves. The primary production that is subsequently fueled by the regenerated N results from the cultivation operations. This synthesis demonstrates the importance of considering the ecological context of bivalve aquaculture when assessing effects on eutrophication, both removal of particulates but also influence on N cycling.

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954 FIGURE CAPTIONS
955
956 **Fig. 1** Cherrystone Inlet, VA. Clam aquaculture operations are delineated by black polygons.
957
958 **Fig. 2** Seasonal dataflow extrapolations of chl in Cherrystone Inlet.
959
960 **Fig. 3** Long-term trends (1989 – 2012) in active aquaculture clam beds in Cherrystone Inlet
961 based on areal photograph analysis for the years 2001 – 2012 combined with data for aquaculture
962 coverage from 1989 – 1997 from Woods (2001).
963
964 **Fig. 4** Benthic respiration rates (a) and net NH_4^+ fluxes (b) scaled to the ecosystem at the
965 uncultivated sediments (gray) and clam beds, including contribution from the clams (i.e.
966 respiration and excretion) (white) and microbial respiration and N mineralization (black).
967
968 **Fig. 5** Annual C and N budget showing fluxes in Mg C or N yr^{-1} associated with the clam beds
969 and water column. Net DIC and DIN fluxes (FLUX), macroalgal primary production (P.P.) and
970 denitrification (DNF) were directly measured (Murphy et al. 2015, Murphy et al. in review) and
971 subsequently scaled here. Clam physiological rates including clam ingestion (ING), respiration

(RESP), excretion (EXC), egestion (EGE), and growth (GROWTH) were modeled and scaled to the standing stock of clams in the system (current study); phytoplankton primary production (P.P.) and the input of DIN from the watershed and Chesapeake Bay were modeled (Kuschner 2015); export of PN and PC via harvest (HARVEST) were provided by the clam growers. *GROWTH here does not account for reproduction or mortality; GROWTH = ING – RESP/EXC – EGE.

Supplementary Fig. S1 Clam tissue dry weight (g) as a function of shell length (mm) measured in clams collected from Cherrystone Inlet in May, July, and November 2013.

Supplementary Fig. S2 Clam oxygen demand (OD) and NH_4^+ flux from a closed-chamber flux experiment conducted in July 2013, in which clams were incubated without sediment. The average ratio of oxygen uptake and NH_4^+release (respiration:excretion) was equal to 7.83, which was used to convert clam respiration rates to excretion rates.

Supplementary Fig. S3 Average seasonal light attenuation (K_d; m^{-1}) measured in 1990-91 (W. Reay, pers. comm.) (black) and 2012 (Murphy et al. 2015) (white). Between the two time periods, light attenuation decreased by 25, 51, and 61% in Spring, Summer, and Fall, respectively.

Figure1_Murphy

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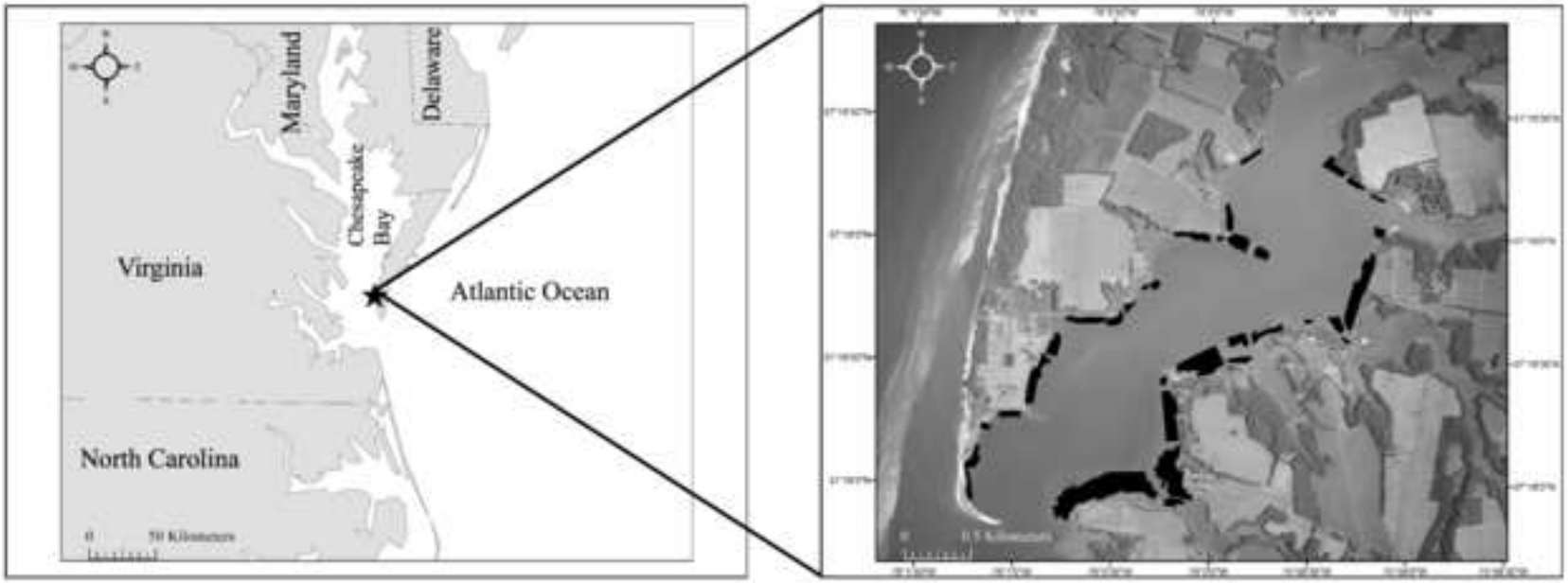

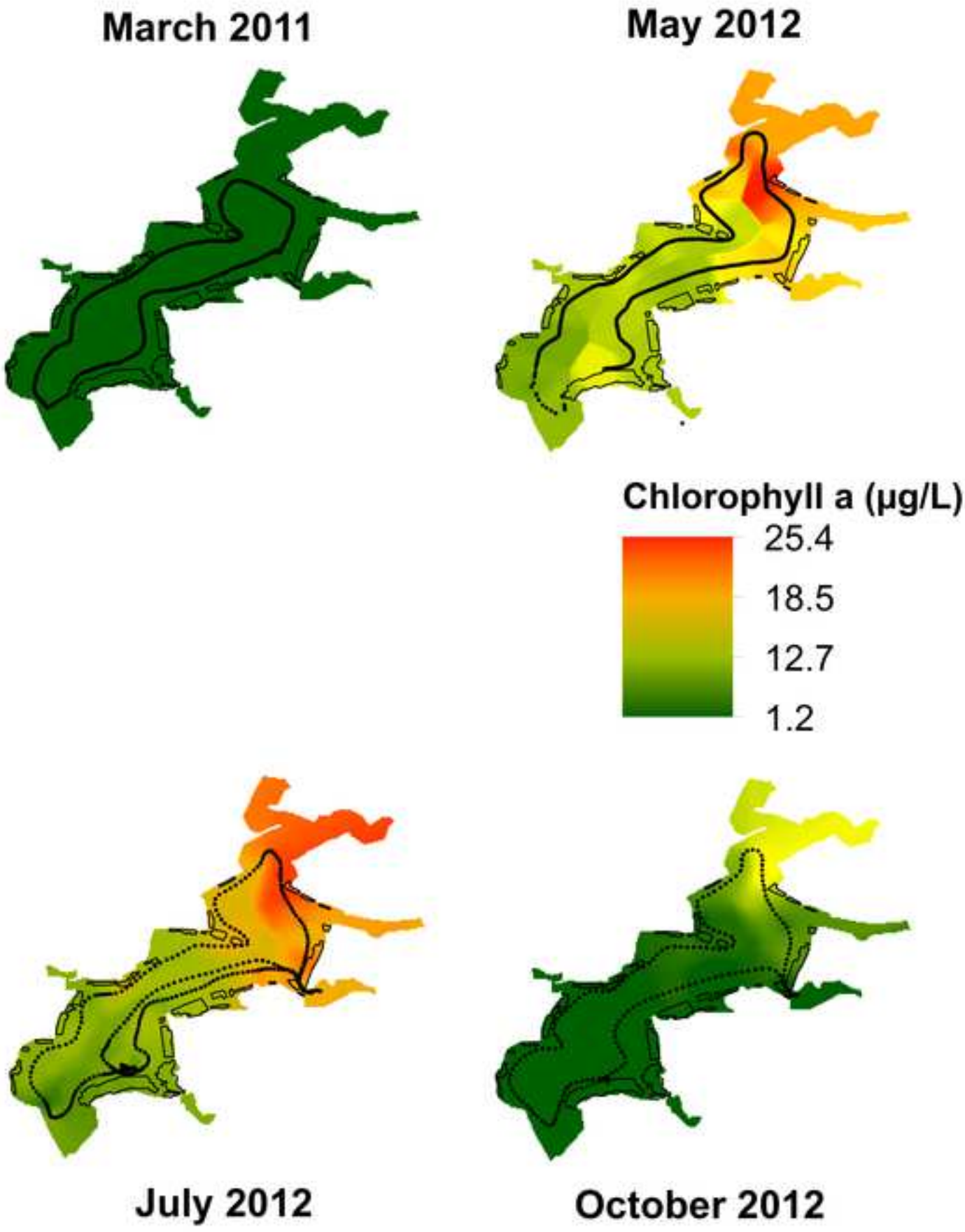

Figure3

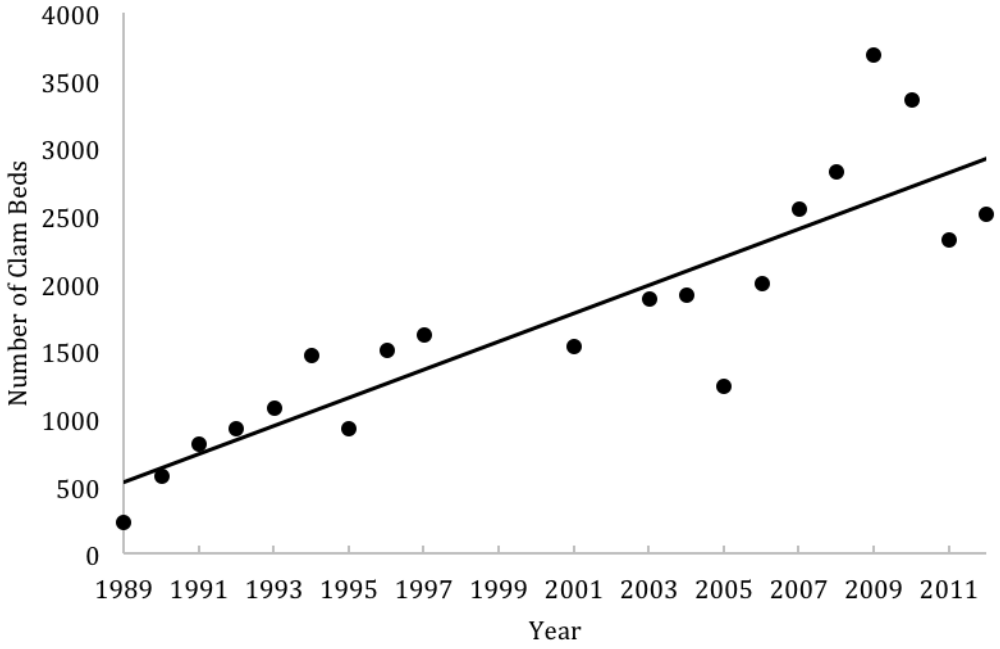
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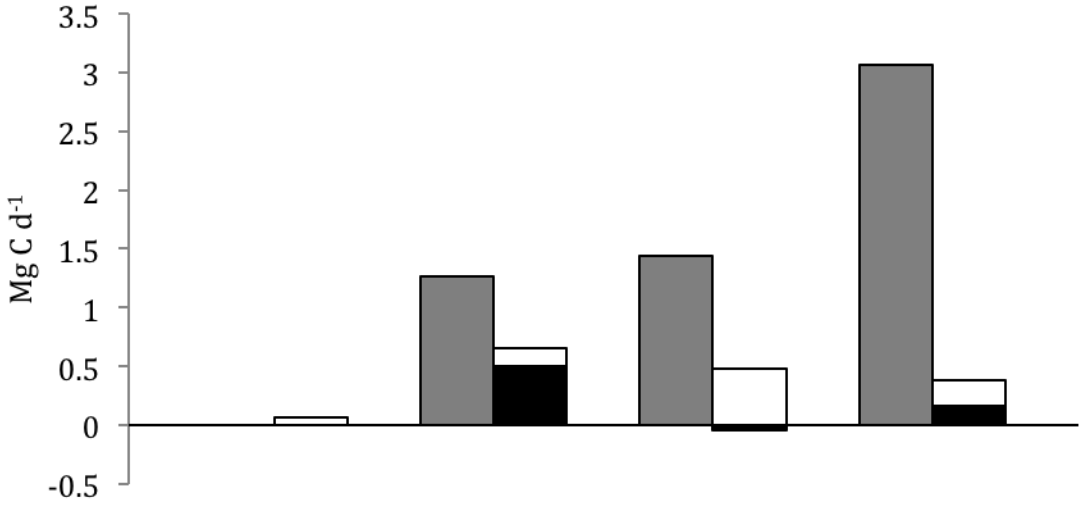
Figure4

a.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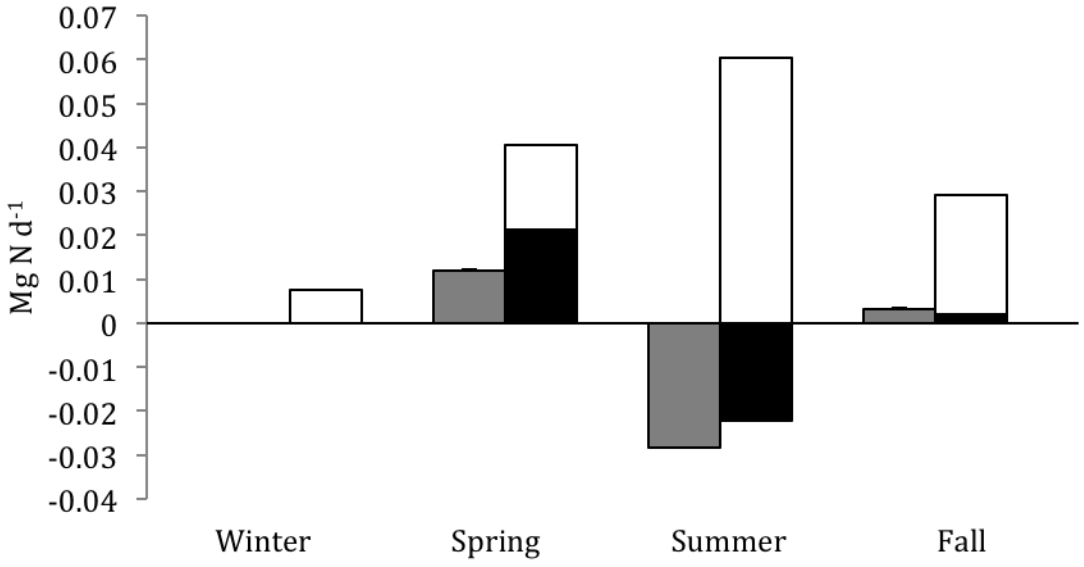
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Figure5_Murphy

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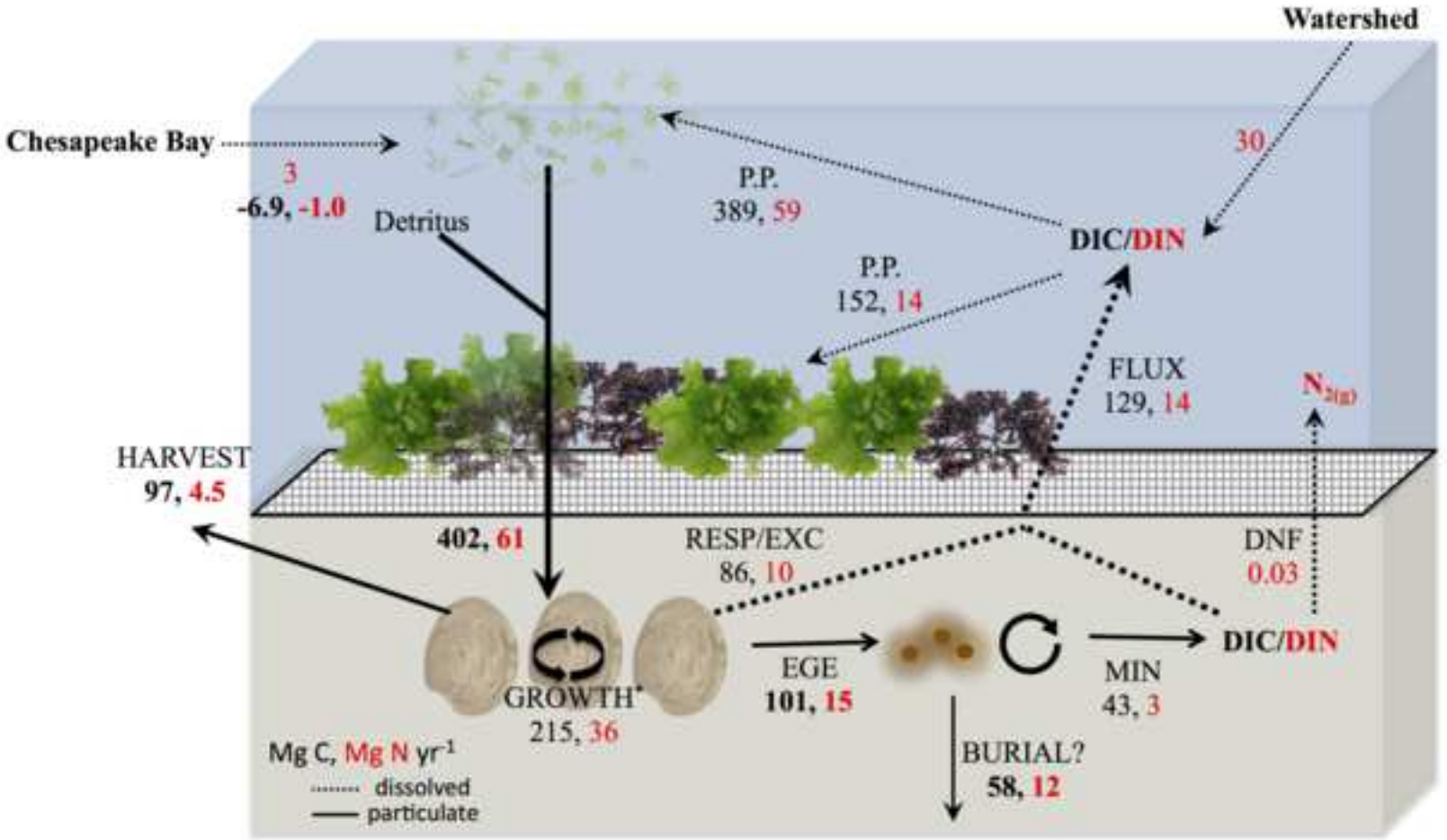


Table 1 Seasonal average water column characteristics in 2012, Cherrystone Inlet.

Season	Salinity	Temperature (°C)	POC (mg l^{-1})	PN (mg l^{-1})	TSS (mg l^{-1})	Chl (ug l^{-1})
dec-feb	22.4	7.1	0.10	0.02	46.9	1.8
mar-may	19.5	16.2	0.87	0.13	77.5	15.2
june-aug	20.9	27.5	0.84	0.13	124.4	14.7
sept-nov	24.6	19.7	0.38	0.06	42.9	6.7

Table2

	Parameter	Seed	Button	Littlenecks	Middlenecks	Total
Size	Avg Length (mm)	12.0	38.5	45.7	56.1	
	Tissue Biomass (gDW ind^{-1})	0.06	0.5	0.9	1.5	
	Shell Biomass (gDW ind^{-1})	0.3	8.8	14.6	26.6	
Standing Stock	Number (ind)	$3.6x10^7$	$6.4x10^7$	$3.5 x10^7$	$9.3 x10^6$	$1.4 x10^8$
	Tissue (Mg C)	0.9	13.4	12.2	5.7	32.1
	Tissue (Mg N)	0.2	3.0	2.8	1.3	7.3
	Shell (Mg C)	1.4	75.3	68.4	32.8	177.9
	Shell (Mg N)	0.02	1.1	1.0	0.5	2.7
Harvested (yr^{-1})	Number (ind)	0	$1.5 x10^6$	$1.3 x10^7$	$1.6 x10^7$	$3.0 x10^7$
	Tissue (Mg C yr^{-1})	0	0.3	4.5	9.5	14.4
	Tissue (Mg N yr^{-1})	0	0.1	1.5	3.1	3.2
	Shell (Mg C yr^{-1})	0	1.7	25.2	55.3	82.2
	Shell (Mg N yr^{-1})	0	0.03	0.4	0.8	1.2

Table 2 Clam size and biomass in Cherrystone Inlet, 2012. Standing stock numbers, C and N content by size category; annual harvest information including total number and C and N removed by harvest.

Table 3 2012 seasonal filtration rates of the standing stock clam population in Cherrystone Inlet including the magnitudes relative to the tidal exchange and volume of the creek.

Season	Total Filtration Rate (m^3 day^{-1})	% Tidal Exchange	% Inlet filtered daily	Time to filter Inlet volume (days)
Winter	0.4×10^6	10%	7%	14.5
Spring	1.6×10^6	37%	26%	3.9
Summer	2.3×10^6	52%	37%	2.7
Fall	2.8×10^6	62%	44%	2.3

Table 4 2012 seasonal average clam bioenergetics (kg C or N day^{-1}) of the total standing stock in Cherrystone Inlet including ingestion, egestion, respiration and excretion, and assimilation. Total annual rates (Mg C or N yr^{-1}) of these physiological processes for the clam population in Cherrystone Inlet are provided.

Season	Ingested		Egested		Respiration/Excretion		Net Assimilation (+ reproduction)[1]	
	C	N	C	N	C	N	C	N
Winter	43.9	6.6	11.0	1.7	59.2	7.6	-26.3	-2.6
Spring	1380.1	208.3	345.0	52.1	147.9	18.9	887.2	137.3
Summer	1905.5	287.6	476.4	71.9	462.6	59.1	966.6	156.6
Fall	1051.2	158.7	262.8	39.7	210.9	26.9	577.5	92.1
Annual (Mg C or N /yr)	401.9	60.7	100.5	15.2	85.5	10.3	215.9	45.5

[1]respiration and excretion has been subtracted from total assimilation rates

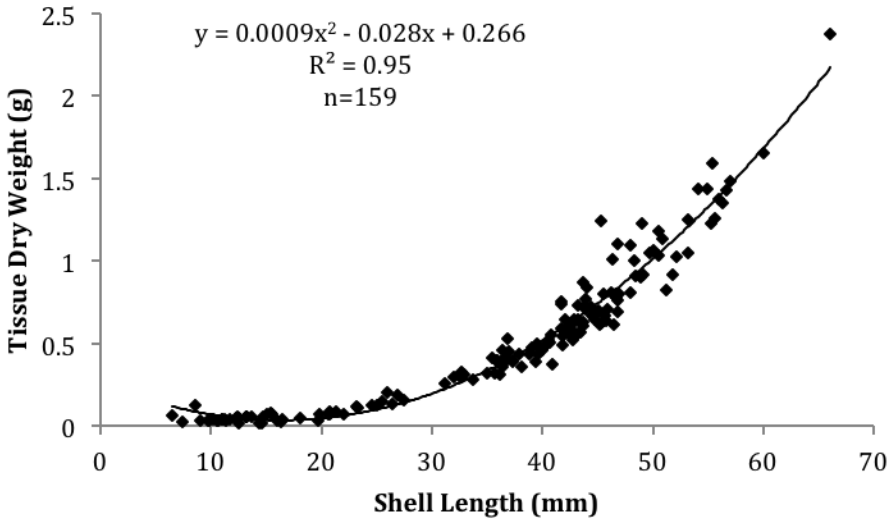
Table 5 Seasonal net primary pelagic production and turnover time in Cherrystone Inlet, derived from the output of an ecosystem model provided by Kuschner (2015), compared to the time it takes the standing clam population to filter the entire system ("Bivalve Clearance Time") and the water residence time of the embayment (Herman et al. 2007).

Season	Phytoplankton Turnover time (d)	Bivalve Clearance Time (d)	Water Residence time (d)
Winter	3.6	14.5	
Spring	1.6	3.9	~2-3
Summer	1.3	2.7	
Fall	3.3	2.3	

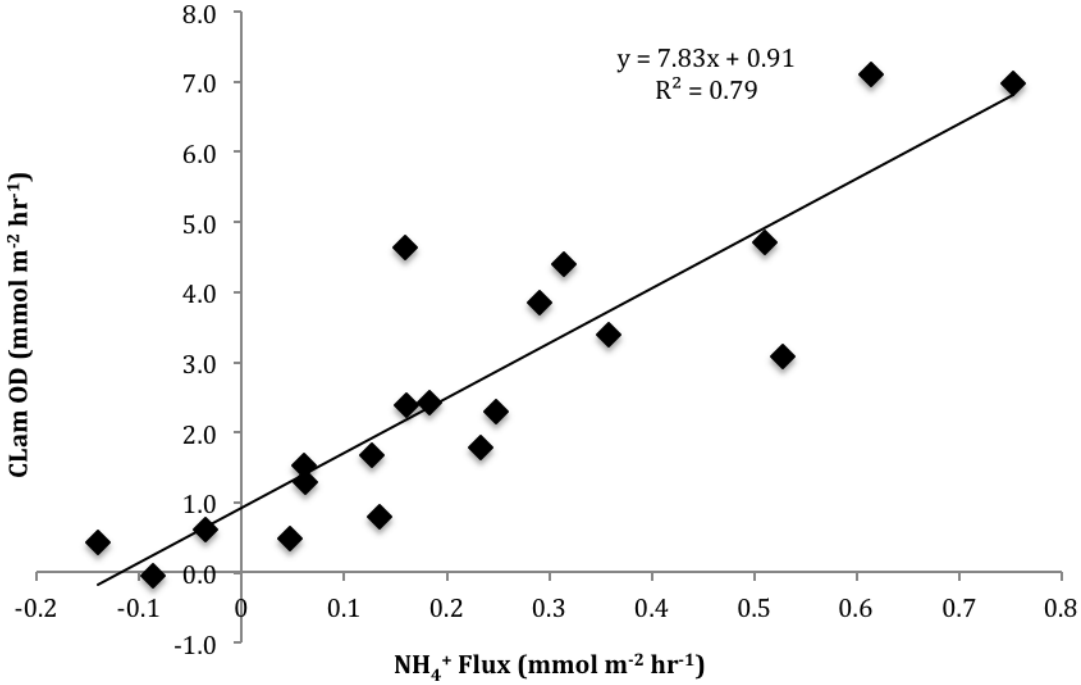
Table 6 Annual primary production (Mg C yr^{-1}) and N demand (Mg N yr^{-1}) for phytoplankton (Kuschner 2015), benthic microalgae (BMA; Reay et al. 1995, Murphy et al. 2015), and macroalgae (Murphy et al. 2015). Also shown are clam ingestion rates and the percent of the phytoplankton production that the clams consume.

	Annual	
	C	N
Phytoplankton	389.0	58.7
BMA (Reay et al. 1995)	298.2	33.1
BMA (Murphy et al. 2015)	1295.6	144.0
Macroalgae	149.4	13.4
Clam Ingestion	401.9	60.7
% of phytoplankton clams ingest	103%	

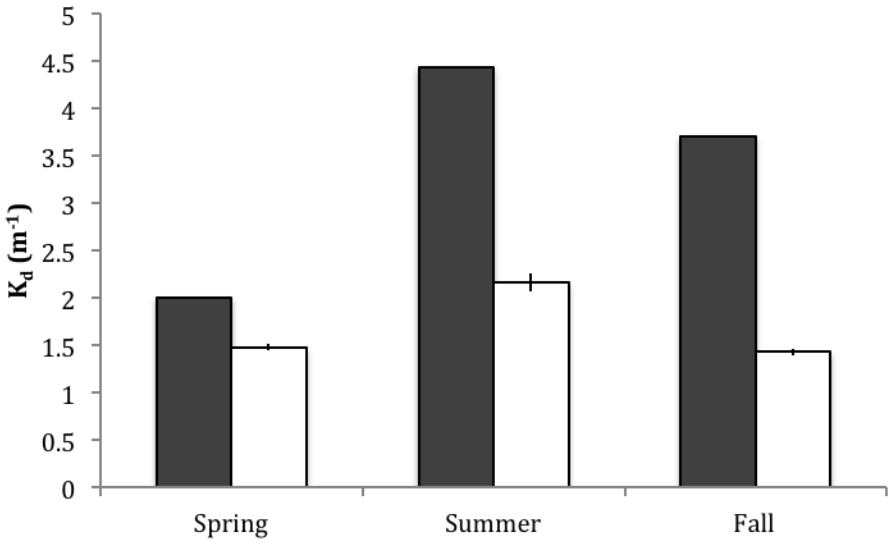
SuppFigure1



SuppFigure2



SuppFigure3



SuppTable1

Clam Physiological Rate	Equation(s)	Measured Variables	Reference(s)
Filtration Rate (FR) (ml ind^{-1} d^{-1})	$FR = FR_{max} * f(T) * f(Sal) * f(TSS)$ $FR_{max} = ((L^{0.96} * T^{0.95})/2.95) * 60 * 24$ $f(T) = 0.277 * \left(1 - \frac{e^{(2(T-T_2))}-1}{e^{(2(T-T_2))}+1}\right) * \left(1 - \frac{e^{(2(T-T_3))}-1}{e^{(2(T-T_3))}-1}\right)$ $f(Sal) = -0.1027 * 10^{-3}S^2 + 0.4144S - 4.302$	T: temperature (°C) L: shell length (mm) S: salinity (ppt)	Doering and Oviatt 1986; Hofmann et al. 2006; Wiseman 2010
Ingestion Rate (I_c, I_N) (g PC or PN ind^{-1} d^{-1})	I_c = FR x chl *a* x 57.214 I_N = FR x chl *a* x 7.025	chl *a*: mean seasonal chl *a* (mg l^{-1})	
Respiration (R) (gDIC ind^{-1} d^{-1})	$R = 24 * (a * W^{0.8184}) * e^{0.1012(T-20)} * \left(\frac{10^{-6}}{22.414}\right) * 12$	a: base respiration rate (200 µl O_2 hr^{-1} gDW^{-1}) W: clam biomass (g DW) T: temperature (°C)	Hofmann et al. 2006; Wiseman 2010
Excretion (U) (gN ind^{-1} d^{-1})	Log U = 0.94 Log W + 1.33	W: clam tissue biomass (g DW)	Srna and Baggaley 1978
Assimilation (A_C, A_N) (gC or gN ind^{-1} d^{-1})	$A_C = C_c$ x 0.75 $A_N = C_N$ x 0.75		Tenore and Dunstan 1973; Kuschner 2015
Egestion (E) (gC or gN ind^{-1} d^{-1})	$E_C = C_c$ x 0.25 $E_N = C_N$ x 0.25		Tenore and Dunstan 1973; Kuschner 2015

Supplementary Table S1. Summary of the equations, variables, and references used to model clam bioenergetics.

Supplementary Table S2. A comparison of water quality parameters collected by dataflow surveys nearby the clam cultivation operations and outside of the operations. Averages and (standard deviations) are provided seasonally.

	May		July		October	
	Inlet	Clam beds	Inlet	Clam beds	Inlet	Clam beds
DO (mg/L)	9.25 (0.47)	9.07 (0.44)	8.09 (0.16)	8.14 (0.17)	8.85 (0.37)	8.66 (0.25)
Turbidity (NTU)	13.15 (6.7)	10.68 (4.1)	23.27 (15.6)	16.29 (6.8)	10.65 (5.3)	8.2 (2.5)
pH	8.19 (0.1)	8.15 (0.1)	7.98 (0.04)	7.99 (0.03)	7.99 (0.06)	7.97 (0.04)
Chl (ug/L)	15.2 (3.4)	13.99 (2.4)	15.5 (4.2)	13.7 (3.3)	7.73 (3.5)	5.85 (2.2)